

## Functional and Adaptive Significance of Primate Pads and Claws: Evidence From New World Anthropoids

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**ABSTRACT** This study tests predicted morphoclines in fingertip morphology among four small-bodied (<1 kg) New World monkeys (*Saimiri sciureus*, *Leontopithecus rosalia*, *Callithrix jacchus*, and *Saguinus oedipus*) in order to test previous functional and adaptive explanations for the evolution of flattened nails, expanded apical pads, and grasping extremities within the Order Primates. Small-bodied platyrrhines which frequently forage among small-diameter substrates are expected to possess 1) relatively expanded apical pads, 2) well-developed epidermal ridges, 3) distally broad terminal phalanges, and 4) reduced flexor and extensor tubercles compared to those species which use large-diameter arboreal supports more frequently for their locomotor and postural behaviors. Results show that as the frequency of small-branch foraging increases among taxa within this sample, relative distal phalanx breadth also increases but distal phalanx length, height, and flexor tubercle size decrease. Moreover, epidermal ridge development becomes more pronounced as the frequency of small-branch foraging increases. Terminal phalanx breadth and epidermal ridge complexity are both positively correlated with apical pad size. The large, flexible apical pad increases stability of the hand and foot on small-diameter arboreal supports because the pad can contact the substrate in several planes which, in turn, enables the pad to resist disruptive forces from different directions by friction and interlocking (Hildebrand, 1995). The observed morphoclines demonstrate that a gradient in form from claw- to nail-like tegulae exists among these taxa. Thus, the distinction between claw- and nail-bearing platyrrhines is essentially arbitrary. These observations corroborate Cartmill's (1972) functional and adaptive model for the loss of claws in primates: namely, expanded apical pads are required for habitual locomotor and postural behaviors on small-diameter supports whereas claws are more useful for positional behaviors on large-diameter substrates. Finally, results from this study support previous suggestions that the keeled tegulae of callitrichines represent a derived postural adaptation rather than a primitive retention from an ancestral eutherian condition. *Am J Phys Anthropol* 106:113–127, 1998. © 1998 Wiley-Liss, Inc.

The evolution of flattened nails on all digits of the hand and foot distinguishes primates from other eutherian orders (Clark, 1936, 1959). Cartmill (1972, 1974) suggested that, although claws are superior to flattened nails for locomotor and postural behaviors on large-diameter vertical arboreal supports, claws are not as useful as

expanded apical pads and flattened nails for locomotion on small-diameter arboreal substrates. Thus, he explained the evolutionary

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replacement of claws with flattened nails as an adaptive transformation enabling early primates to forage successfully for insects among the slender terminal branches of trees and shrubs (Cartmill, 1972, 1974). New World primates of the family Callitrichidae, however, possess claws on all digits except the hallux, but certain callitrichids such as *Saguinus oedipus* spend much of their time foraging for fruits and insects within the "terminal branch niche" (Garber, 1980; Garber and Sussman, 1984). Claws, therefore, do not appear to hinder the movements of these primates on small-diameter substrates, leading Cartmill (1985, p. 83) to conclude that "the clawlessness of more typical primates . . . thus presents a persistent theoretical problem" (see also Dagosto, 1988).

Claws and nails have been characterized as discrete character states, although both LeGros Clark (1936) and Thorndike (1968) showed that "a gradient in form from claw to nail, rather than a clear dichotomy between the two, is seen among living primates" (Thorndike, 1968, p. 251). Evidence from the nails and claws of birds (Bock and Miller, 1959; Feduccia, 1993), rodents (Haffner, 1996), carnivores (VanValkenburgh, 1987; Bryant et al., 1996), and other mammals (Macleod and Rose, 1993) reveals that interspecific variation in fingertip morphology is functionally related to interspecific variation in locomotor, postural, and manipulatory behavior. Hence, morphoclines in apical pad morphology and distal phalanx architecture can be used to test functional and adaptive hypotheses concerning the evolution of primate cheiridial form. The objective of this study is to test predicted morphoclines in apical pad and distal phalanx morphology among small-bodied New World monkeys which differ significantly from one another in their foraging behaviors in order to test Cartmill's (1972, 1974, 1985) functional and adaptive model for the evolution of flattened nails, expanded apical pads, and grasping extremities in primates.

## PREDICTIONS

### Apical pad morphology

The apical pads of primates bearing flattened ungulae are relatively expanded and exhibit well-developed papillary ridges (Mar-

tin, 1990). The papillary ridges serve not only to improve the frictional properties of the digital skin but also to increase the skin's sensitivity to tactile stimuli (Cauna, 1954; Napier, 1980; Loesch and Martin, 1984). The frictional properties of the ridges derive primarily from their ability to produce surface interlocking (Whipple, 1904; Cartmill, 1974). The importance of well-developed friction pads for small-branch foragers is clearly illustrated by Cartmill (1985), who showed that grasping digits allow a climbing mammal to exert torques opposite to those produced by gravity when pitching over on small-diameter substrates. The ridges are also important for tactile sensitivity, since pressure on the elevated ridges applies a mechanical stimulus to tactile receptors called Meissner's corpuscles, rapidly adapting mechanoreceptors located underneath the basins between the papillary ridges which signal stimulus onset and offset (Cauna, 1954, 1956; Burgess and Perl, 1973; Halata, 1975).

Cartmill's model predicts that New World primates such as squirrel monkeys (*Saimiri sciureus*), which frequently (>80%) forage and feed among small-diameter (<3 cm) arboreal supports of variable orientation (Fleagle et al., 1981; Boinski, 1989; Fontaine, 1990), should have relatively large apical pads bearing numerous papillary ridges in order to increase the interlocking properties of their grasping fingers. In contrast, small-bodied monkeys such as common marmosets (*Callithrix jacchus*), which forage for exudates by clinging to large-diameter (>15 cm) vertical supports and travel primarily by leaping between such supports (Lacher et al., 1984; Sussman and Kinzey, 1984; Garber, 1992), would be expected to have relatively small apical pads and poorly developed papillary ridges. The cotton-topped tamarin *S. oedipus*, which forages on large- and small-diameter supports (Garber, 1980; Garber and Sussman, 1984), and the golden lion tamarin *Leontopithecus rosalia*, which forages frequently on small- and medium-sized (3–12 cm) horizontal supports (Peres, 1989; Garber, 1992; Stafford et al., 1996), would both be expected to possess apical pads and papillary ridges that are

more well developed than those of *Callithrix* but less so than those of *Saimiri*.

### Terminal phalanx shape

The falculae of most arboreal mammals (e.g., *Tupaia*, *Distoechurus*) are characterized by both a superficial corneous layer derived from a basal matrix of germinal cells and a deep corneous layer derived from a terminal matrix of germinal cells (Clark, 1936). The evolution of flattened ungulae in the majority of primates is associated with the loss of the terminal matrix and deep corneous layer. A number of extant primates bearing claw-like tegulae do, however, retain both a terminal matrix and deep corneous layer (Clark, 1936). Clark (1936) showed that, among the platyrrhines he included for study, *C. jacchus* had the most well-developed deep layer, which comprises about 17% of the total claw depth. The deep layer of *S. oedipus* represents about 10% of the total claw depth and *Cebus albifrons* possesses only a rudimentary deep layer (Thorndike, 1968). The studies of both Clark (1936) and Thorndike (1968) illustrate clear morphoclines in nail and claw ultrastructure among platyrrhines and their analyses are not repeated here. The following predictions relate variation in morphology of the platyrrhine terminal phalanx to the aforementioned variations in platyrrhine substrate use and nail and claw form.

Arboreal mammals bearing well-developed falculae typically possess terminal phalanges with enlarged flexor and extensor tubercles, which increase the lever arms for the long flexors and extensors, respectively, acting at the distal interphalangeal joints (Clark, 1936; Rosenberger, 1977). The large lever arm for the long flexor tendon permits powerful interlocking of the claw with the substrate, required for clinging and climbing behaviors on large-diameter vertical arboreal supports where the central angle subtended by the hands and feet is less than 180° (Cartmill, 1979). The large lever arm for the long extensor permits powerful dorsiflexion of the claw during quadrupedal walking, running, and bounding on these large-diameter substrates. The distal phalanx of arboreal mammals bearing falculae is also compressed radioulnarly and high dorsopal-

marly in order to accommodate the keeled corneous sheath (Clark, 1936).

The flexor and extensor tubercles are both reduced in arboreal primates that utilize grasping extremities for locomotor and postural behaviors on small-diameter substrates (Clark, 1936). Arboreal mammals bearing grasping extremities can wrap their fingers and toes around the substrate, effectively subtending a central angle exceeding 180°. The adduction force applied to the support by the digit is exerted by all of the phalangeal segments across all of the interphalangeal joints, not just the distal interphalangeal joints (Preuschoft, 1970, 1973). Thus, compared to clawed arborealists that possess a very well-developed lever arm for the long flexor tendon at the distal interphalangeal joint, clawless mammals exhibit a relatively reduced flexor tubercle on the distal phalanx. Finally, the distal phalanx of arboreal mammals with flattened ungulae is, in contrast to that of clawed mammals, expanded radioulnarly and shortened dorsopalmarly in order to accommodate a flattened superficial corneous layer and broad apical pad.

*C. jacchus*, which spends the overwhelming majority of its feeding time clinging to large-diameter vertical arboreal supports (Table 1), would be expected to possess relatively large flexor tubercles and radioulnarly compressed and dorsopalmarly expanded terminal phalanges related to its claw-like tegulae. *S. sciureus*, which is more of a small-branch forager, would be expected to have reduced flexor and extensor tubercles and a more radioulnarly expanded and dorsopalmarly compressed distal phalanx in order to support both a relatively broad nail and apical pad. *S. oedipus*, which forages on small- and large-diameter supports, and *L. rosalia*, which forages on large- and medium-diameter branches, would both be expected to possess flexor tubercles that are somewhat intermediate in relative size between those of *Saimiri* and *Callithrix*. Callitrichids do not use their keeled tegulae during quadrupedal walking and running (Rosenberger, 1977; Rosenberger and Stafford, 1994) and they would therefore not be expected to possess very large extensor tubercles used for claw dorsiflexion. *L. rosa-*

TABLE 1. Sample sizes ( $n$  = number of skeletal specimens, number of cadaver specimens) and adaptive profiles for the four New World monkey species included for study

Species (n)	Body mass <sup>a</sup>	Diet <sup>b</sup>	Substrate preference <sup>b</sup>
<i>Saimiri sciureus</i> (10, 2)	825 g.	insects (70%) fruit	horizontal, oblique <3 cm diameter
<i>Saguinus oedipus</i> (7, 2)	485 g.	insects (40%) gum, <sup>c</sup> fruit	horizontal, oblique/vertical <3 cm, >15 cm <sup>c</sup>
<i>Leontopithecus rosalia</i> (9, 2)	600 g.	insects (50–70%) nectar, fruit	horizontal 3–15 cm diameter
<i>Callithrix jacchus</i> (10, 2)	275 g.	gum (<70%) insects	vertical >15 cm diameter

<sup>a</sup> Pooled-sex values from Fleagle (1988).

<sup>b</sup> Data from Fleagle et al. (1981), Fleagle (1988), Garber (1992), Stafford et al. (1996), and Dietz et al. (1997).

<sup>c</sup> Frequencies of exudate feeding associated with the use of large-diameter vertical supports increase during the dry season, approaching 50% compared to only 20–30% in the wet season (Garber, 1992).

*lia* frequently forages for cryptic insect prey concealed in bark and under leaves by probing with its elongate fingers (Garber, 1992; Dietz et al., 1997). This taxon would, like other arboreal mammalian extractive foragers (e.g., *Daubentonia*, *Dactylopsila*, *Dactylonax*), be expected to possess relatively elongate terminal phalanges related to the use of its fingers as probes (Godinot, 1992).

## MATERIALS AND METHODS

### Sample

Morphoclines in apical pad and terminal phalanx morphology were examined in a total of 36 skeletal specimens and eight cadaver specimens of *S. sciureus*, *S. oedipus*, *L. rosalia*, and *C. jacchus* (Table 1). These taxa were chosen for analysis because they are similarly sized (<1 kg) and their cheiridial dimensions can therefore be compared within a “narrow allometric” context (sensu Smith, 1980). The skeletal specimens studied are housed in the National Museum of Natural History, Smithsonian Institution. Cadaver specimens of *Saimiri* and *Leontopithecus* are also from the National Museum of Natural History, whereas specimens of *Saguinus* and *Callithrix* are from the University of Tennessee at Knoxville. Body weights, diets, and substrate preferences for these taxa are shown in Table 1.

### Histology

Apical pad morphology was examined in all four species by severing the pad from the volar surface of the third manual distal phalanx in one male and one female fluid-preserved specimen representing each species. A tissue sample was removed from the

middle of each pad where the papillary ridges run proximodistally in order to ensure that similar regions of the apical pad were examined in each individual. These tissue specimens were then washed in tap water for 24 hours and placed in a 70% ethanol solution. Specimens were later dehydrated using a graded series of ethanol solutions, cleared, and embedded in paraffin following the general procedure described by Humason (1972). Once specimens were embedded in paraffin blocks they were sectioned at 10  $\mu$ m in the transverse plane using a rotary microtome. Thin sections were then mounted on slides and stained using Weigert's hematoxylin counterstained with picroponceau in order to visualize structure of the dermis and epidermis (Humason, 1972). Stained sections were viewed and photographed through a high-powered Olympus stereo light microscope.

### Osteometrics

The terminal phalanx from the third finger of one hand representing each skeletal specimen was traced in lateral and palmar views using a Zeiss stereo microscope with camera lucida attachment. Ten points were then digitized on these outlines using SigmaScan<sup>TM</sup> digitizing software in order to calculate the following linear distances shown in Figure 1: terminal phalanx length (L), from the most distal point on the proximal articular surface to the distal tip of the bone; height of the phalangeal body (MSH), from the dorsal and palmar borders of the phalanx at approximately midshaft; extensor lever arm (ETUB), from the most distal point on the proximal articular surface to



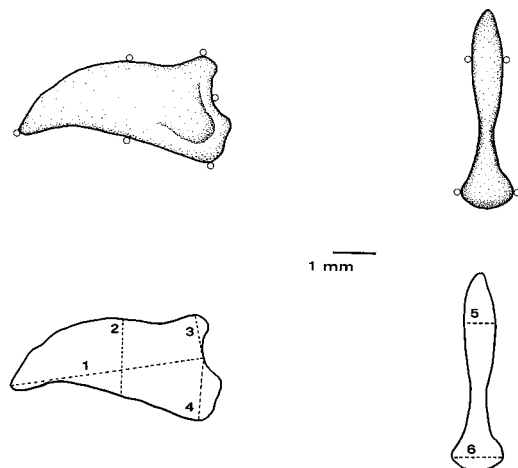


Fig. 1. Terminal phalanx from the third manual digit of *Callithrix jacchus* in lateral (left column) and palmar (right column) views showing the ten points digitized on the camera lucida tracings (top row) and the six linear distances calculated between the ten digitized points (bottom row).

the dorsal border of the extensor process; flexor lever arm (FTUB), from the most distal point on the proximal articular surface to the palmar border of the extensor process; apical tuft breadth (TUFW), from the radial and lateral borders of the distal end at its widest diameter; base breadth (BASW), from the radial and lateral borders of the phalangeal base. These linear dimensions were chosen for analysis because they capture functionally relevant aspects of distal phalanx shape discussed earlier. The raw linear dimensions were expressed as log-shape ratios for statistical analysis following the procedure described by Mosimann and James (1979), Falsetti et al. (1993), and Jungers et al. (1996).

#### Statistical analyses

Nonparametric statistical tests were used for interspecific comparisons of log-shape ratio values in order to eliminate distributional and dispersion assumptions within this sample. Kruskal-Wallis tests were first used to investigate interspecific differences in these shape ratio values and Mann-Whitney U tests were then used for pairwise between-species comparisons, following Sokal and Rohlf (1981) and Zar (1984). A multivariate discriminant analysis was also

performed on the logged ratio values in order to test for interspecific differences using the multivariate dataset. A multivariate analysis of variance (MANOVA) was the preferred technique for this analysis, since the groups were defined a priori (Neff and Marcus, 1980). Log-shape variables were also tested for correlations with size by generating Spearman-rank correlations between the log-shape ratios and the log-size (geometric mean) variable.

## RESULTS

### Apical pad morphology

The epidermal structures referred to here are named according to the terminology utilized by Martin (1990, p. 502). Apical pads of *C. jacchus* differ from those of the other three taxa primarily in being markedly compressed radioulnarly relative to their dorsopalmar height (Fig. 2). The volar apical pad skin of both *Callithrix* and *L. rosalia* exhibits undulating papillary ridges which typically correspond to intermediate ridges (= glandular ridges of Halata, 1975) that penetrate into the dermis (Fig. 3a,b). The intermediate ridges of *Callithrix* form elongate, finger-like papillae on the most volar tip of the pad, whereas they are relatively reduced on the radial and ulnar sides of the pad. Many sections of *Callithrix* volar skin exhibit intermediate ridges that are widely spaced and sparsely distributed. *Leontopithecus* also has sparsely distributed intermediate ridges and the basins between the papillary ridges are rather low and flat (Fig. 3b). Epidermal ridge development appears to be correlated, for the most part, with the relative size of the apical pad in these two species.

The volar apical pad skin of *S. oedipus* and *S. sciureus*, like that of both *Callithrix* and *Leontopithecus*, exhibits undulating papillary ridges (Fig. 3c,d). The intermediate ridges of *Saguinus* are, however, more well-developed than those of both *Callithrix* and *Leontopithecus*. Furthermore, the apical pad of *Saguinus* is expanded radioulnarly compared to those of both *Leontopithecus* and *Callithrix* (Fig. 2). Specimens of *Saimiri* exhibit well-developed papillary ridges and elongate intermediate ridges that are comparable in morphology to those of *Saguinus*

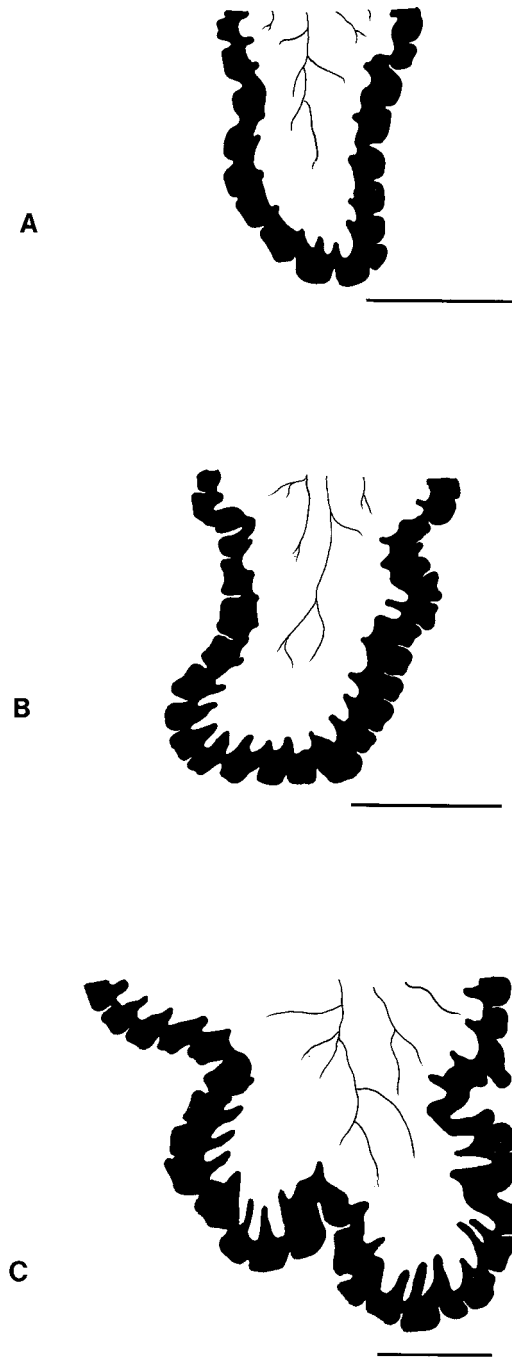


Fig. 2. Tracings of dorsopalmar sections through the apical pad of the third finger in A: *Callithrix jacchus*, B: *Saguinus oedipus*, and C: *Saimiri sciureus* showing the radioulnarly compressed pad of *Callithrix* and more radioulnarly expanded pads of *Saguinus* and *Saimiri*. The epidermis is shaded and the dorsal surface of each section faces toward the top of the page whereas the palmar surface of each section faces toward the bottom of the page. Scale bars = 1 mm.

(Fig. 3d). The basins between the papillary ridges correspond to deeply projecting limiting ridges (= adhesive ridges of Halata, 1975) which, although elongate, do not protrude so deeply into the dermis as the intermediate ridges. The intermediate ridges of *Saimiri* are considerably more well developed than those of the other three taxa studied. Moreover, apical pads of *Saimiri* are much broader radioulnarly than those of the other three platyrrhines examined (Fig. 2).

#### Terminal phalanx shape

Kruskal-Wallis tests show that terminal phalanges of the four platyrrhine taxa included for analysis differ significantly from one another in relative size of the flexor tubercle, breadth and height of the phalangeal body, breadth of the phalangeal base, and length of the terminal phalanx (Figs. 4, 5; Tables 2, 3). The log-shape variables are not significantly correlated with log-size (Table 4), indicating that these ratios are discriminating between taxa primarily on the basis of shape differences. Pairwise comparisons and examination of the raw data show that *Saimiri* has the relatively smallest flexor tubercle of all the taxa, whereas *Callithrix* has the relatively largest flexor tubercle (Figs. 4; Tables 2, 3). *Saguinus* and *Leontopithecus* possess flexor tubercles that are somewhat intermediate in size between those of *Saimiri* and *Callithrix* and, in fact, do not differ significantly from one another in this measurement (Tables 2, 3). *Saimiri* also has a very dorsopalmarly compressed and bilaterally expanded phalangeal body, whereas that of *Callithrix* is very high dorsopalmarly and compressed radioulnarly (Figs. 4, 5a,b). The phalangeal body of *Saguinus* differs significantly from that of *Callithrix* in being more dorsopalmarly compressed and radioulnarly expanded but differs from that of *Saimiri* in being more expanded dorsopalmarly and compressed radioulnarly (Table 3; Figs. 4, 5a,b).

The morphoclines observed among these taxa in relative breadth of the distal phalanx are also observed in relative breadth of phalangeal base. *Saimiri* has the broadest (radioulnarly) base of all the taxa and *Callithrix* has the relatively narrowest phalangeal base (Table 2; Figs. 4, 5c). *Saguinus*

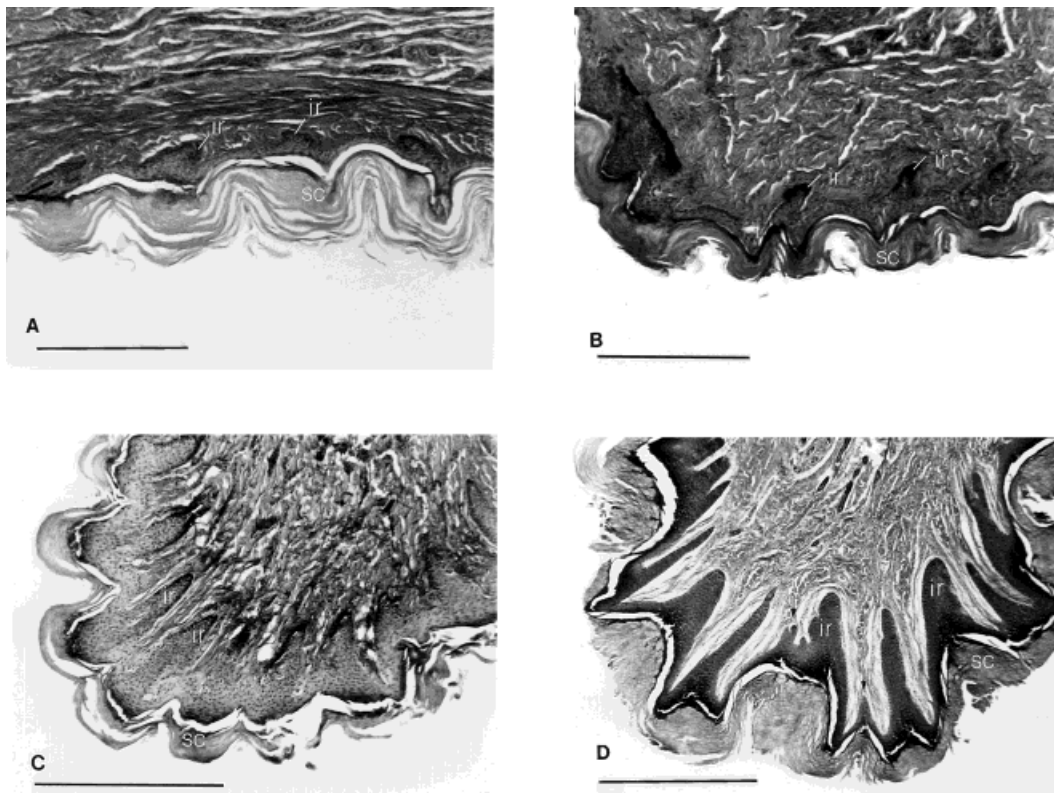


Fig. 3. Photomicrographs of dorsopalmar sections through the apical pad of the third finger in **A:** *Callithrix jacchus* ( $\times 140$ ; scale bar = .25 mm), **B:** *Leontopithecus rosalia* ( $\times 140$ ; scale bar = .25 mm), **C:** *Saguinus oedipus* ( $\times 120$ ; scale bar = .50 mm), and **D:** *Saimiri sciureus* ( $\times 80$ ; scale bar = .50 mm). Note the undulating stratum corneum (sc) of each species and the deeply projecting intermediate ridges (ir) of *Saguinus* and *Saimiri*. The arrows in D point to the limiting ridges of *Saimiri*.

differs significantly from *Saimiri* in having a slightly narrower base but differs significantly from *Callithrix* (and *Leontopithecus*) in having a relatively wider base (Table 3; Fig. 5). Finally, these four small-bodied platyrrhines also differ significantly from one another in relative length of their third distal phalanx. *Leontopithecus* differs significantly from the other taxa in having a relatively elongate terminal phalanx, whereas *Saimiri* has the relatively shortest terminal phalanx of all the taxa studied (Tables 2, 3; Figs. 4, 5d). *Callithrix* and *Saguinus*, which do not differ significantly from one another in this respect, possess terminal phalanges that are intermediate in length between those of *Saimiri* and *Leontopithecus* (Tables 2, 3; Fig. 5). *Leontopithecus* has been noted previously as having very elongate forelimb elements (e.g., Dykyj, 1982;

Rosenberger and Stafford, 1994; Aronsen, 1997) and it is therefore not surprising that this taxon has very elongate terminal phalanges related to its extractive foraging habits.

The morphoclines observed among the four taxa in the univariate analyses are also observed in the multivariate analysis. The MANOVA is highly significant (Wilkes-Lambda = 10.76,  $P < .001$ ) and classified 97% of the cases correctly. The first discriminant axis shows a strong negative correlation with breadth of the phalangeal base and strong positive correlation with height of the phalangeal body (Table 5). Thus, *Saimiri*, which has a broad phalangeal base and dorsopalmarly compressed phalangeal body (Table 2; Fig. 4), has low scores on this axis (Fig. 6), whereas *Callithrix* and *Leontopithecus*, which both have a radioulnarly com-

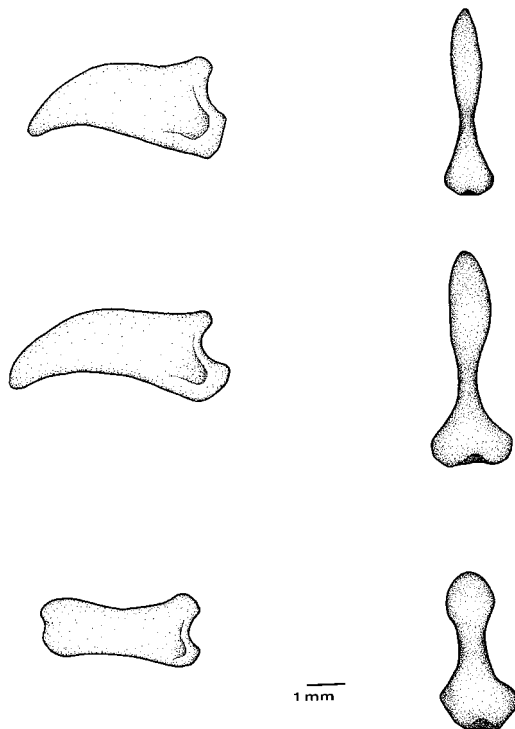


Fig. 4. Lateral (left column) and dorsal (right column) views of the third manual terminal phalanx in *Callithrix jacchus* (top row), *Saguinus oedipus* (middle row), and *Saimiri sciureus* (bottom row).

pressed phalangeal base and dorsopalmarly expanded phalangeal body (Table 2; Fig. 4), have high scores on this axis (Fig. 6). *Saguinus*, which exhibits a pattern of distal phalanx morphology that is somewhat intermediate in form between that of *Saimiri* and *Callithrix*, has intermediate scores on this axis (Fig. 6). The second discriminant axis shows a strong negative correlation with phalangeal length (Table 5). This axis separates *Leontopithecus*, which has a relatively elongate third manual distal phalanx (Table 2; Fig. 5), from the other three species, which tend to have shorter terminal phalanges compared to those of the golden lion tamarin (Fig. 6).

## DISCUSSION

### Evolution of platyrrhine pads and claws

Garber (1980) showed that the keeled tegulae of *S. oedipus* do not hinder the movements of this species on small-diam-

eter substrates. This study reveals that *Saguinus* possesses apical pads and epidermal ridges that are relatively well developed compared to those of other callitrichids (e.g., *Callithrix*, *Leontopithecus*). The proficiency of *Saguinus* on slender arboreal supports can therefore be explained by the fact that its apical pads and terminal phalanges are quite similar in morphology to those of other small-branch foragers (e.g., *Saimiri*). The results of this study, therefore, corroborate Cartmill's (1972, 1974, 1985) functional and adaptive model for the origin of expanded apical pads, flattened nails, and grasping extremities within the Order Primates. Specifically, results presented here indicate that relatively expanded apical pads and broad, flat ungulae characterize those species that frequently forage within the "small-branch niche" of the arboreal milieu. Conversely, claw-like tegulae and reduced apical pads are more useful than flattened ungulae and expanded apical pads for habitual locomotor and postural behaviors on large-diameter arboreal supports.

The morphoclines in terminal phalanx and apical pad morphology observed among the callitrichines examined in this study raise the question of what pattern might be phylogenetically primitive for callitrichines and which patterns might therefore represent derived conditions. Garber concluded that, "based on the dental anatomy, dietary patterns, and positional behavior of extant tamarins and marmosets, *Saguinus* appears to be the most ecologically generalized" (Garber, 1992, p. 479) of the callitrichines. *C. jacchus* is clearly a more dedicated gummivore than *Saguinus* sp. and *Leontopithecus* is a specialized extractive forager. The most parsimonious transformation scheme, in light of Garber's (1992) behavioral data and recent phylogenetic evidence (e.g., Schneider et al., 1993; Schneider and Rosenberger, 1996), is that the well-developed apical pads and broad terminal phalanges of *S. sciureus* approximate the primitive platyrrhine condition. The more keeled tegulae of *S. oedipus* are therefore derived from *Saimiri*-like ungulae in relation to the evolution of seasonal exudate feeding. Thus, the morphology of *S. oedipus* tegulae approximates the condition primitive for callitrichines. The morphology



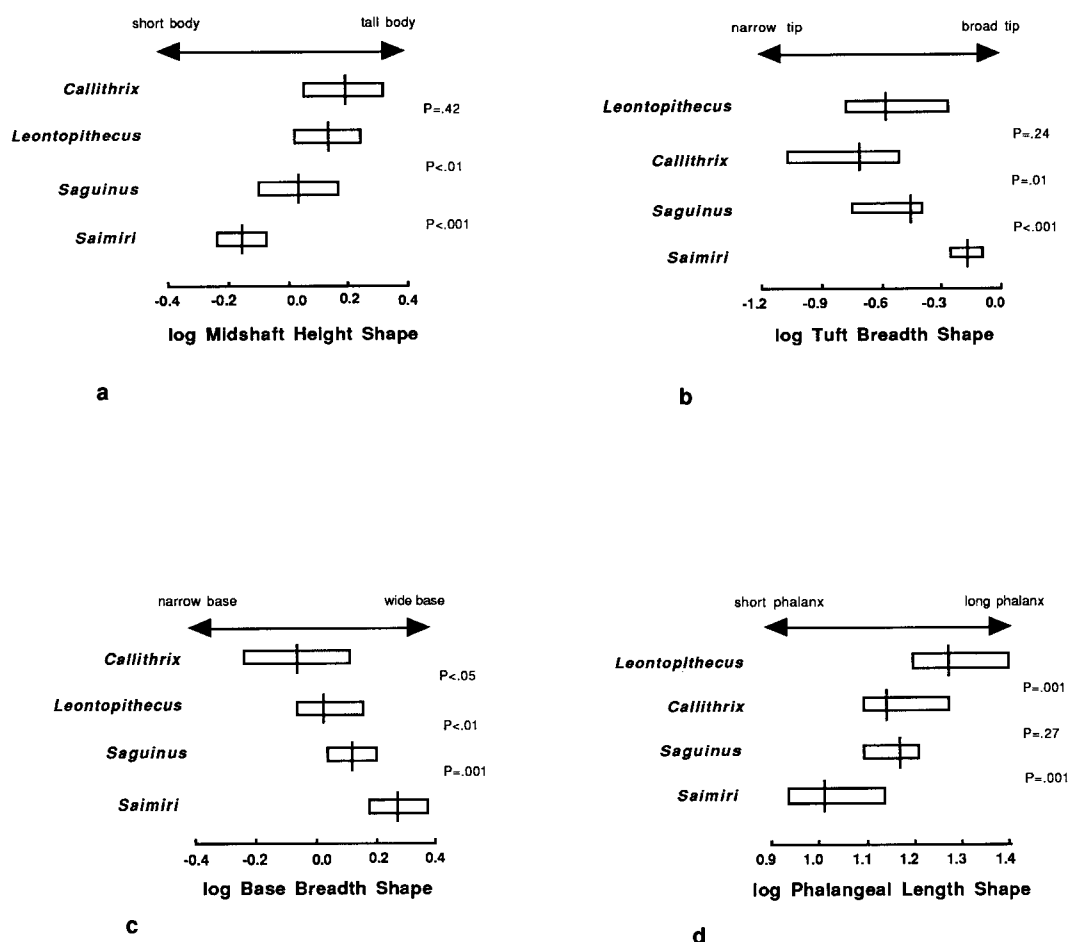


Fig. 5. Univariate plots of log-shape ratio values for **a**: relative midshaft height, **b**: relative tuft breadth, **c**: relative base breadth, and **d**: relative phalangeal length in four New World anthropoids. The horizontal bars represent the range of values for each species and the vertical bars represent the median values for each species. P-values are shown for Mann-Whitney comparisons between species.

TABLE 2. Summary statistics for log-shape ratio values showing the mean and (standard deviation) for each variable for each species\*

	<i>Saimiri sciureus</i>	<i>Saguinus oedipus</i>	<i>Leontopithecus rosalia</i>	<i>Callithrix jacchus</i>
ETUB	-.57 (.07)	-.62 (.12)	-.67 (.06)	-.61 (.08)
FTUB	-.04 (.09)	-.19 (.10)	-.17 (.21)	.07 (.05)
MSH	-.15 (.05)	.02 (.07)	.14 (.07)	.17 (.08)
TUFW	-.17 (.04)	-.50 (.11)	-.58 (.16)	-.70 (.15)
BASW	.29 (.07)	.12 (.05)	.01 (.07)	-.07 (.08)
L	1.01 (.06)	1.16 (.04)	1.28 (.06)	1.14 (.04)

\* Measurement abbreviations are explained in the text.

of *Callithrix* and *Leontopithecus* tegulae represent derived character states, related to the evolution of habitual gummivory and extractive foraging behaviors in these two taxa, respectively.

Hershkovitz (1970) and Napier (1980) suggested that the claws of callitrichids are a mechanical obstruction to their fingertips that interfere with both the use of their fingertips as tactile organs and with full phalangeal flexure during single-handed (i.e., prehensile) grips. Lemelin (1994) and Lemelin and Grafton (in press) have, however, recently shown that *Saguinus* is as competent as *Saimiri* at single-handed pre-

TABLE 3. Results of between-species pairwise comparisons (Mann-Whitney U-tests) for the log-shape variables included for analysis<sup>a</sup>

	FTUB ( $H = 24.42$ , $P < .001$ )	MSH ( $H = 26.42$ , $P < .001$ )	TUFW ( $H = 24.05$ , $P < .001$ )	BASW ( $H = 27.24$ , $P < .001$ )	L ( $H = 26.27$ , $P < .001$ )
Ss vs. So	**	***	***	***	***
Ss vs. Lr	*	***	***	***	***
Ss vs. Cj	***	***	***	***	***
So vs. Lr	ns	**	ns	**	***
So vs. Cj	***	**	**	***	ns
Lr vs. Cj	**	ns	ns	*	***

<sup>a</sup> Results of Kruskal-Wallis tests are shown in parentheses. No pairwise tests were executed for ETUBL because there was no significant difference among the species sampled in this log-shape variable ( $H = 6.74$ ,  $P = .08$ ).

Ss = *Saimiri sciureus*, So = *Saguinus oedipus*, Lr = *Leontopithecus rosalia*, Cj = *Callithrix jacchus*.

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

ns =  $P > .05$ .

TABLE 4. Spearman's rank correlation coefficients ( $\rho$ ) between the log-shape variables included in the discriminant analysis and the log-size variable\*

	Correlation with log-size
ETUB	-.11 (.49)
FTUB	-.13 (.41)
MSH	-.05 (.77)
TUFW	-.03 (.84)
BASW	.12 (.47)
L	.27 (.11)

\*  $\rho$  values are shown above  $P$ -values, which are in parentheses.

TABLE 5. Correlations (loadings) between dependent variables and factor scores for each discriminant axis of the discriminant analysis (MANOVA) shown in Figure 6

	Axis 1	Axis 2	Axis 3
MSH	.53	.27	-.25
BASW	-.52	-.49	.48
TUFW	-.44	-.40	-.38
L	.43	-.85	.10
FTUB	.33	.73	.15
ETUB	-.09	.22	.08

hension of small food items such as berries and crickets. Results presented in this study again show that similarities in prehensile capabilities between *Saguinus* and *Saimiri* can be explained at least in part by the fact that both *Saguinus* and *Saimiri* have relatively broad apical pads and well-developed epidermal ridges. Given the fact that *Callithrix* has relatively reduced apical pads it

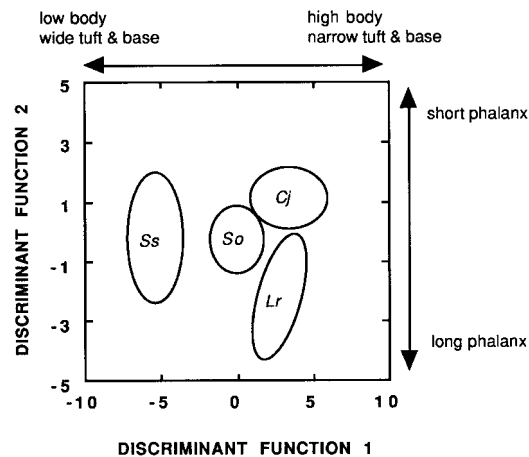


Fig. 6. Bivariate plot of the first two discriminant axes for a discriminant analysis of third terminal phalanx log-shape ratio values in four New World anthropoids. The centroids enclose the range of values for each species. Ss = *Saimiri sciureus*, So = *Saguinus oedipus*, Cj = *Callithrix jacchus*, Lr = *Leontopithecus rosalia*.

would be interesting to compare the prehensile capabilities of this taxon with those of *Saguinus*. If expanded apical pads are a prerequisite for tactile sensitivity and prehensility, as some workers have suggested (see below), then we might expect *Callithrix* to exhibit less prowess at one-handed prehension of small food items compared to *Saguinus*.

This study also demonstrates that terms such as "claws" and "nails" do not accurately reflect the variation in apical pad and terminal phalanx morphology seen among the four monkeys studied. It is obvious from Figure 5 that there is no single bony feature

that can be used to divide this sample into claw- and nail-bearing forms. That is, any distinction would be an arbitrary one. Rather, as Thorndike (1968) noted for primates as a group, a gradient in form from nail- to claw-like tegulae exists among these small-bodied New World primates. These data also reveal that differences in anthropoid apical pad and terminal phalanx morphology are tightly correlated with subtle differences in platyrrhine substrate preferences. Recent morphofunctional studies of platyrrhine postcranial morphology (e.g., Davis, 1996, and references therein) have shown that postcranial morphology and positional behavior do not always form an exclusive one-to-one relationship within this group. The present study serves as an example of platyrrhine postcranial morphology closely matching that expected under a predictive functional and adaptive model. This is, however, a relatively narrow comparison among only four taxa. Future analyses should be directed at investigating similar patterns in other monophyletic groups of arboreal mammals that exhibit diversity in their substrate preferences and cheiridial morphology (e.g., burramyid marsupials, loriform primates).

Rosenberger (1977) and Szalay (1981) argued that the keeled tegulae of callitrichids are not homologous with those of other clawed arboreal mammals such as squirrels and tree shrews. They noted that callitrichids, unlike *Sciurus* and *Tupaia*, lack sesamoids at their distal interphalangeal joints and also have reduced extensor tubercles on their distal phalanges. Quantitative results from this study show that the taxa included for analysis do indeed have reduced extensor tubercles (Table 2). Moreover, these taxa do not differ significantly from one another in the relative size of their extensor tubercles. For example, both *Saimiri*, which bears flattened ungulae, and *Callithrix*, which possesses keeled tegulae, have extensor tubercles that are similar in relative size. The large extensor tubercles of squirrels and tree shrews enable them to forcefully retract their claws from arboreal supports during quadrupedal locomotion. The claws of callitrichids, however, do not contact arboreal substrates during locomotion

(Rosenberger and Stafford, 1994). The results presented in this study therefore support both Garber's (1992) hypothesis that callitrichid tegulae are a derived postural adaptation related to exudate feeding and Rosenberger's (1977) hypothesis that callitrichid tegulae are neither morphologically homologous nor functionally analogous to those of clawed arborealists such as *Tupaia*.

#### The functional significance of primate volar skin morphology

Results from this study suggest that well-developed papillary ridges characterize small-branch foragers (e.g., *Saguinus*, *Saimiri*), whereas these ridges are not so well developed in taxa that habitually use large-diameter substrates (e.g., *Callithrix*). What functional advantage(s) do these epidermal ridges confer on a small-branch forager? The first hypothesis is that the ridges enhance tactile sensitivity by sending elongate intermediate ridges into the dermis (Schlaginhaufen, 1905; Clark, 1936; Loesch and Martin, 1984). The intermediate ridges serve as levers that transmit a mechanical stimulus from the papillary ridge to nerve endings located within the dermal crypts alongside the intermediate ridges (Cauna, 1954). The papillary ridges are, therefore, sensors that enable an arboreal primate to rapidly assess the size, orientation, flexibility, and movement of the substrate. The second hypothesis is that the primary role of the papillary ridges is to enhance pad friction by surface interlocking (Whipple, 1904; Cartmill, 1974, 1985). The dorsally projecting intermediate ridges simply correspond to the size of the palmarly protruding papillary ridges, a fact that led Napier (1980) to liken the papillary ridges to icebergs. Thus, selection favoring well-developed papillary ridges for surface interlocking would produce correlated evolution of well-developed intermediate ridges.

Comparative evidence suggests that the latter hypothesis is preferable. Humans have very keen tactile sensitivity but have relatively flat papillary ridges (Fig. 7). Our intermediate ridges are numerous but, relative to the overall size of our apical pads, they are not very elongate and do not project very deeply into the dermis (Fig. 7). Our

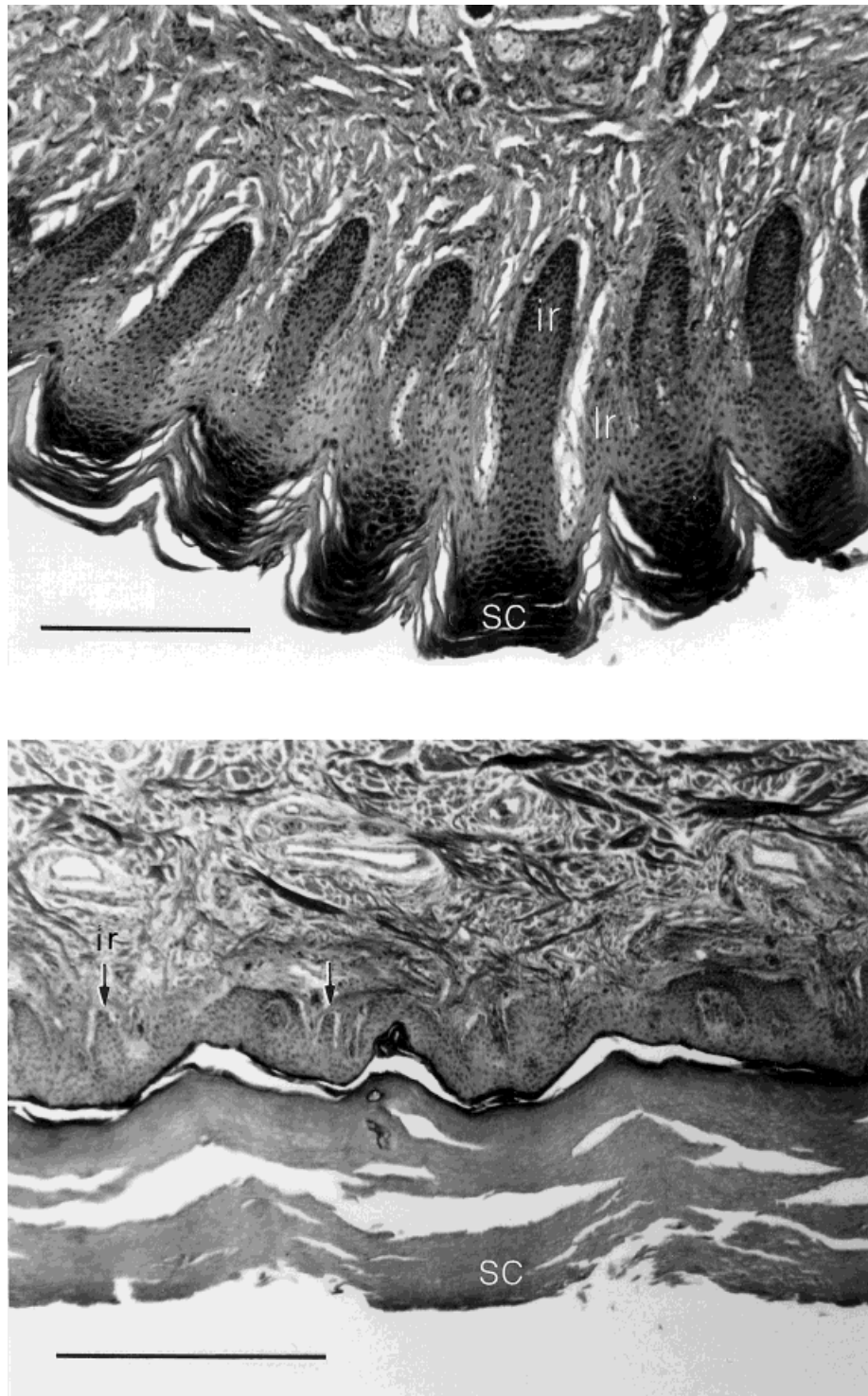


Fig. 7. Photomicrographs of dorsopalmar sections through the pollical apical pad in *Didelphis virginiana* (**top**;  $\times 120$ ; scale bar = .25 mm) and *Homo sapiens* (**bottom**;  $\times 80$ ; scale bar = .50 mm). Note that in *Didelphis* the stratum corneum (sc) bears undulating papillary ridges which give rise to deeply penetrating intermediate ridges (ir) whereas in *Homo* the intermediate ridges (ir; arrows) are reduced relative to the papillary ridges at the skin's surface.



enhanced tactile sensitivity derives from numerous rapidly adapting (Meissner's corpuscles) and slowly adapting (Merkel endings) mechanoreceptors located within the dermis close to the intermediate and lateral ridges (Winkelmann, 1963; Kandel et al., 1991). Hence, well-developed papillary ridges are not necessarily a prerequisite for tactile sensitivity. This hypothesis is corroborated further by the morphology of raccoon glabrous volar skin. The raccoon's palmar pads are richly innervated by slowly adapting mechanoreceptors located between undulating limiting ridges (Munger and Pubols, 1972). The papillary ridges and associated intermediate ridges are, however, poorly developed in raccoon digital skin (see Munger and Pubols, 1972).

Additional evidence to support this mechanical argument is provided by the marsupial *Didelphis*. This climbing opossum has a divergent grasping hallux like primates and also exhibits well-developed papillary ridges associated with elongate intermediate ridges on its thumb and finger pads (Fig. 7). *Didelphis*, however, possesses arm and hand somatic sensory projections within its neocortex that are poorly developed compared to those of both *Procyon* and *Homo* (Welker and Seidenstein, 1959; Johnson, 1977; Kandel et al., 1991). In other words, the brain of *Didelphis*, in contrast to that of both *Homo* and *Procyon*, is relatively unspecialized for tactile reception. The well-developed papillary and intermediate ridges of *Saimiri*, *Saguinus*, and *Didelphis*, and the more poorly developed papillary and intermediate ridges of *Homo* and *Procyon*, suggest that well-developed papillary ridges evolved in the majority of primates in order to facilitate the mechanical, rather than sensory, properties of the apical pads.

#### A scenario for primate claw loss

If keeled tegulae do not hinder the movements of arboreal mammals on small-diameter arboreal substrates, then why would evolution favor the loss of claws on all digits of the primate hand and foot? I propose that 1) the *habitual* use of small-diameter supports by the earliest primates favored the evolution of relatively large and broad (radioulnarly) apical pads on the fingers and toes

for the mechanical reasons discussed below, 2) the overall size and breadth of the apical pads are increased by increasing the breadth of the terminal phalanges, so that selection for large, broad apical pads favored the evolution of broad terminal phalanges in the earliest primates, 3) broad, flat ungulae on the hands and feet are a correlated by-product of having broad terminal phalanges on the fingers and toes, that is, the three-dimensional shape of the superficial and deep corneous layers conform to the shape of the terminal phalanx, and 4) primates retained papillary ridges on their fingers and toes from a clawed arboreal ancestor but these ridges were more well-developed in primates due to an overall increase in apical pad size.

This adaptive hypothesis is supported by the fact that *Anolis* lizards living in a small-branch environment have relatively broader apical pads on their toes than their conspecifics living in a large-branch environment (Losos et al., 1997). A functional explanation underlying this phenomenon is offered by Hildebrand (1995), who suggested that a large, flexible apical pad increases stability of the digit on small-diameter arboreal supports because the pad can contact the substrate in several planes. This in turn enables the pad to resist, via friction, adhesion, or surface interlocking, disruptive forces from different directions. Cartmill (1974) has shown that increasing the size of the apical pad does not increase the pad's frictional properties (Amonton's first law). A larger pad bearing interlocking or adhesive asperities (e.g., setae, scales, or papillary ridges) does, however, increase stability of the pad on the support because the number of contact points between these asperities and the substrate is increased. This mechanical model explains why both reptiles and mammals living in a small-branch environment have enlarged apical pads on their fingers and toes, even though both have quite different patterns of volar skin structure and innervation.

#### CONCLUSIONS

This study was undertaken in order to test predicted morphoclines in hand apical pad and terminal phalanx morphology

among four small-bodied (<1 kg) New World monkeys. Results show that as the frequency of small-branch foraging increases among taxa within this sample relative distal phalanx breadth increases but distal phalanx length, height, and flexor tubercle size decrease. Moreover, epidermal ridge development becomes more pronounced as the frequency of small-branch foraging increases. Terminal phalanx breadth and epidermal ridge complexity are both positively correlated with apical pad size in this sample of New World monkeys. Apical pad size in turn appears to be positively correlated with stability of the digit on small-diameter supports. The platyrrhines studied exhibit continuous interspecific variation in these hand features, revealing that there is no clear morphological basis for distinguishing between claw- and nail-bearing New World monkeys. These observations corroborate Cartmill's (1972, 1974, 1985) functional and adaptive model for the loss of claws in primates. That is, relatively expanded apical pads and broad, flat ungulae characterize those species that frequently forage within the "small-branch niche" of the arboreal milieu, whereas keeled tegulae and reduced apical pads are observed in species which exhibit a preference for positional behaviors on medium- and large-diameter arboreal supports. Moreover, these results support previous suggestions that the keeled tegulae of callitrichines are a derived postural adaptation related to the evolution of seasonal exudate feeding in the last common ancestor of the Callitrichinae.

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#### LITERATURE CITED

- Aronsen GP (1997) The functional anatomy of the forelimb in *Callimico goeldii* and *Leontopithecus rosalia*: A study integrating kinematic and morphological data. *Am. J. Phys. Anthropol. Suppl.* 24:68.
- Bock WJ, and Miller W (1959) The scansorial foot of the woodpeckers with comments on the evolution of perching and climbing feet in birds. *Am. Mus. Nat. Hist. Novitates* 1931:1-45.
- Boinski S (1989) The positional behavior and substrate use of squirrel monkeys: Ecological implications. *J. Hum. Evol.* 18:659-677.
- Bryant HN, Russell A, Laroia R, and Powell G (1996) Claw retraction and protraction in the carnivora: Skeletal microvariation in the phalanges of the Felidae. *J. Morph.* 229:289-308.
- Burgess A, and Perl C (1973) Cutaneous mechanoreceptors and nociceptors. In A Iggo (ed): *Handbook of Sensory Physiology*, Vol. II. New York: Springer-Verlag, pp 29-78.
- Cartmill M (1972) Arboreal adaptations and the origin of the order Primates. In R Tuttle (ed): *Functional and Evolutionary Biology of Primates*. Chicago: Aldine-Atherton, pp 97-122.
- Cartmill M (1974) Pads and claws in arboreal locomotion. In FA Jenkins Jr (ed): *Primate Locomotion*. New York: Academic Press, pp 45-83.
- Cartmill M (1979) The volar skin of primates: Its frictional characteristics and their functional significance. *Am. J. Phys. Anthropol.* 50:497-510.
- Cartmill M (1985) Climbing. In M Hildebrand, D Bramble, K Liem, and D Wake (eds): *Functional Vertebrate Morphology*. Cambridge: Harvard University Press, pp 73-88.
- Cauna N (1954) Nature and functions of the papillary ridges of the digital skin. *J. Anat.* 119:449-468.
- Cauna N (1956) Nerve supply and nerve endings in Meissner's corpuscles. *Am. J. Anat.* 99:315-350.
- Clark WE LeGros (1936) The problem of the claw in primates. *Proc. Zool. Soc. Lond.* 1936:1-24.
- Clark WE LeGros (1959) *The Antecedents of Man*. Edinburgh: Edinburgh University Press.
- Dagosto M (1988) Implications of postcranial evidence for the origin of euprimates. *J. Hum. Evol.* 17:35-56.
- Davis LC (1996) Functional and phylogenetic implications of ankle morphology in Goeldi's monkey (*Callimico goeldii*). In M Norconk, A Rosenberger, and P Garber (eds): *Adaptive Radiations of Neotropical Primates*. New York: Plenum Press, pp 133-156.
- Dietz J, Peres CA, and Pinder L (1997) Foraging ecology and use of space in wild golden lion tamarins (*Leontopithecus rosalia*). *Am. J. Primatol.* 41:289-305.
- Dykj D (1982) Allometry of trunk and limbs in New World monkeys. Doctoral Dissertation, City University of New York.

- Falsetti AB, Jungers WL, and Cole TM (1993) Morphometrics of the callitrichid forelimb: A case study in size and shape. *Int. J. Primatol.* 14:551–572.
- Feduccia A (1993) Evidence from claw geometry indicating arboreal habits of *Archaeopteryx*. *Science* 259:790–793.
- Fleagle JG, Mittermeier R, and Skopec A (1981) Differential habitat use by *Cebus apella* and *Saimiri sciureus* in central Surinam. *Primates* 22:361–367.
- Fontaine R (1990) Positional behavior in *Saimiri boliviensis* and *Ateles geoffroyi*. *Am. J. Phys. Anthropol.* 82:485–508.
- Garber PA (1980) Locomotor behavior and feeding ecology of the Panamanian tamarin (*Saguinus oedipus geoffroyi*). *Int. J. Primatol.* 1:185–201.
- Garber PA (1992) Vertical clinging, small body size, and the evolution of feeding adaptations in the Callitrichinae. *Am. J. Phys. Anthropol.* 88:469–482.
- Garber PA, and Sussman R (1984) Ecological distinctions between sympatric species of *Saguinus* and *Sciurus*. *Am. J. Phys. Anthropol.* 65:135–146.
- Haffner M (1996) A tendon-locking mechanism in two climbing rodents, *Muscardinus avellanarius* and *Microtus minutus* (Mammalia, Rodentia). *J. Morph.* 229:219–227.
- Halata M (1975) The mechanoreceptors of the mammalian skin: Ultrastructure and morphological classification. *Adv. Anat. Embryol. Cell Bio.* 50:3–75.
- Hershkovitz P (1970) Notes on Tertiary platyrrhine monkeys and a description of a new genus from the late Miocene of Columbia. *Folia Primatol.* 12:1–37.
- Hildebrand M (1995) Analysis of Vertebrate Structure. New York: John Wiley & Sons, Inc.
- Humason GL (1972) Animal Tissue Techniques. San Francisco: W.H. Freeman.
- Johnson JI Jr. (1977) Central nervous system of marsupials. In D Hunsaker II (ed): The Biology of Marsupials. New York: Academic Press, pp 159–278.
- Jungers WL, Falsetti AB, and Wall C (1995) Shape, relative size, and size-adjustments in morphometrics. *Yrbk. Phys. Anthropol.* 38:137–161.
- Kandel ER, Schwartz JH, and Jessell TM (1991) Principles of Neural Science. Norwalk: Appleton and Lange.
- Lacher T, Bouchardet G, Alves C, and Magalhaes-Castro B (1984) Parasitism of trees by marmosets in a central Brazilian gallery forest. *Biotropica* 16:202–209.
- Lemelin P (1994) Manual grasping behavior in *Saguinus midas* and its relevance for early primate evolution. *Am. J. Phys. Anthropol.* 18:128–129.
- Lemelin P, and Grafton B (in press) Grasping performance in *Saguinus midas* and the evolution of hand prehensility in primates. In E Strasser and J Fleagle (eds): Primate Locomotion: Recent Advances. New York: Plenum Press.
- Loesch DZ, and Martin NG (1984) Finger ridge patterns and tactile sensitivity. *Ann. Hum. Biol.* 11:113–124.
- Losos JB, Warheit KI, and Schoener TW (1997) Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* 387:70–73.
- MacLeod N, and Rose KD (1993) Inferring locomotor behavior in paleogene mammals via eigenshape analysis. *Am. J. Sci.* 293A:300–355.
- Martin RD (1990) Primate Origins and Evolution. New Jersey: Princeton University Press.
- Mosimann JE, and James FC (1979) New statistical methods for allometry with applications to Florida red-winged blackbirds. *Evolution* 23:444–459.
- Munger BL, and Pubols LM (1972) The sensorineural organization of the digital skin of the raccoon. *Brain Behav. Evol.* 5:367–393.
- Napier JR (1980) Hands. New Jersey: Princeton University Press.
- Neff NA, and Marcus LF (1980) A Survey of Multivariate Methods for Systematics. New York: American Museum of Natural History.
- Peres CA (1989) Exudate-eating by wild golden lion tamarins, *Leontopithecus rosalia*. *Biotropica* 21:287–288.
- Preuschoft H (1970) Statische untersuchungen an den fussen der primaten. Teil II: statik des ganzen fusses. *Z. Anat. Entw. Gesch.* 131:156–192.
- Preuschoft H (1973) Functional anatomy of the upper extremity. In G Bourne (ed): The Chimpanzee. Baltimore: University Park Press, pp 34–120.
- Rosenberger A (1977) *Xenothrix* and ceboid phylogeny. *J. Hum. Evol.* 6:461–481.
- Rosenberger A, and Stafford B (1994) Locomotion in captive *Leontopithecus* and *Callimico*: A multimedia study. *Am. J. Phys. Anthropol.* 94:379–394.
- Schlaginhaufen O (1905) Das hautleistebsystem der primatenplanta unter mitberucksichtigung der palma. *Morph. Jahrb.* 34:1–125.
- Schneider H, and Rosenberger AL (1996) Molecules, morphology, and platyrrhine systematics. In M Norconk, A Rosenberger, and P Garber (eds): Adaptive Radiations of Neotropical Primates. New York: Plenum Press, pp 3–19.
- Schneider H, Schneider MPC, Sampaio MIC, Harada ML, Stanhope M, and Goodman M (1993) Molecular phylogeny of the New World monkeys (Platyrrhini, Primates). *Mol. Phyl. Evol.* 2:225–242.
- Smith RJ (1980) Rethinking allometry. *J. Theor. Biol.* 87:97–111.
- Sokal R, and Rohlf F (1981) Biometry. New York: W.H. Freeman.
- Stafford BJ, Rosenberger AL, Baker AJ, Beck BB, Dietz JM, and Kleiman DG (1996) Locomotion of golden lion tamarins (*Leontopithecus rosalia*). In M Norconk, A Rosenberger, and P Garber (eds): Adaptive Radiations of Neotropical Primates. New York: Plenum Press, pp 111–132.
- Sussman RW, and Kinzey WG (1984) The ecological role of the Callitrichidae: A review. *Am. J. Phys. Anthropol.* 64:419–449.
- Szalay FS (1981) Functional analysis and the practice of the phylogenetic method as reflected by some mammalian studies. *Am. Zool.* 21:37–45.
- Thorndike E (1968) A microscopic study of the marmoset claw and nail. *Am. J. Phys. Anthropol.* 28:247–262.
- Van Valkenburgh B (1987) Skeletal indicators of locomotor behavior in living and extinct carnivores. *J. Vert. Paleont.* 7:162–182.
- Welker WI, and Seidenstein S (1959) Somatic sensory representation in the cerebral cortex of the raccoon. *J. Comp. Neur.* 111:469–501.
- Whipple IL (1904) The ventral surface of the mammalian cheiridium, with special reference to conditions found in man. *Z. Morph. Anthropol.* 7:261–368.
- Winkelman RK (1963) Nerve endings in the skin of primates. In J Buettner-Janusch (ed): Evolutionary and Genetic Biology of Primates, Vol. 1. New York: Academic Press, pp 229–259.
- Zar JH (1984) Biostatistical Analysis. Englewood Cliffs, NJ: Prentice-Hall.